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Cretocycas yezonakajimae gen. et sp. nov., a Permineralized Cycad Petiole from the Upper Cretaceous of Hokkaido[1)]

Makoto NISHIDA[a], Akira YOSHIDA[a] and Harufumi NISHIDA[b]

[a]Research Institute of Evolutionary Biology, 2-4-28 Kamiyoga, Setagaya-ku, Tokyo, 158 JAPAN;
[b]International Budo University, 841 Shinkan, Katsu-ura, Chiba, 299-52 JAPAN

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A new genus and species of the Cycadaceae is described based on a permineralized petiole from the Upper Cretaceous of Hokkaido, Japan. The vascular bundles are arranged in an inverted omega shape composed of 33 strands. Each bundle has a centrarch xylem. The outer cortex consists of evenly distributed fibers and parenchyma cells. This is the first record of a permineralized cycad petiole from the Mesozoic of Japan and adjacent lands. (Continued from Nishida et al., Res. Inst. Evolut. Biol. Sci. Rep. 8: 11–18, 1995)

Introduction

The oldest fossil records of Cycadales occur from the Carboniferous of England and the USA. The Palaeozoic cycad records are all impression or compression fossils of megasporophylls (Pomel 1849, Cridland and Morris 1960, Mamay 1973, 1976, Zhu and Du 1981, Kerp 1983, Gillespie and Pfefferkorn 1986), microsporophylls forming a staminate cone (Taylor 1970), and foliages (Sze 1953, Du and Zhu 1982, Gao and Thomas 1989, Kapool et al. 1991). Permineralized fossils appear first from the Triassic, and increase in number in subsequent periods. They are *Michelilloa* from the Triassic of Argentina (Archangelsky and Brett 1963), *Lyssoxylon* from the Triassic of Arizona, USA (Gould 1971), *Antarcticycas* from the Triassic of Antarctica (Smoot et al. 1985), *Aricycas* and *Charmorgia* from the Triassic of USA (Ash 1985), *Fascisvarioxylon* from the Jurassic of India (Jain 1964), *Cycadinorachis* from the Jurassic of India (Sharma 1973, Suther et al. 1986), *Sanchucycas* from the Lower Cretaceous of Japan (Nishida et al. 1991), *Menucoa* from the Tertiary of Argentina (Petriella 1969) and *Bororoa* from the Tertiary of Argentina (Petriella 1972). Most are permineralized stems except for a cycadean petiole, *Cycadinorachis*.

This paper describes a permineralized cycad petiole from the Upper Cretaceous (Turonian-Coniacian) of Hokkaido, Japan. This is the first permineralized cycad petiole from the Mesozoic of Japan. The fossil was compared to petioles of all living cycad genera except *Chigua* (Stevenson 1990) which is restricted to the Columbian Andes. The anatomy of living cycad petioles will be published elsewhere (Nishida and Yoshida in press).

Materials and Methods

Specimen No. 890712 is a petiole in a sandy calcareous nodule collected by Mr. Isamu Nakajima of Mikasa City, Hokkaido, in the riverbed upstream of Tengubashi bridge crossing the Obirashibe river at Kawakami, Obira Town, Hokkaido. Fossil-contain-

ing nodules are known to have been eroded from the Upper Cretaceous Middle or Upper Yezo Groups (Turonian-Coniacian) which are widely distributed along upstream of Obirashibe river based on associated marine fauna (Shimizu et al. 1953).

The nodule was slabbed into pieces without surface cleaning. Micropreparations were made by peel technique (Joy et al. 1956) using 1.8% hydrochloric acid as an etching reagent.

The type specimen and micropreparations are housed in the Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University.

Results

Taxonomic treatment

Class Gymnospermopsida

Order Cycadales

Family Cycadaceae

Genus *Cretocycas* Nishida, A. Yoshida & H. Nishida gen. nov.

Type species. *C. yezonakajimae* Nishida, A. Yoshida & H. Nishida sp. nov.

Diagnosis of the genus Permineralized Cycad rachis showing internal structures. Vascular bundles arranged in inverted omega shape. Each bundle encircled by bundle sheath. Xylem centrarch with less-developed centrifugal (phloem) side. Cortex double layered; outer consisting of abundant fibers and small amount of evenly-distributed parenchyma cells; inner cortex and pith consisting of parenchyma, nests of fibers and dispersed mucilage canals. Vascular strands located on dorsal side of venter of inverted omega-shaped arrangement have 2–3-layered sclereids in outer (abaxial) side of phloem and outside bundle sheath.

Etymology The genus name originates from the Cretaceous and the genus *Cycas*.

***Cretocycas yezonakajimae* Nishida, A. Yoshida & H. Nishida sp. nov.**

Species diagnosis As that of the genus.

Etymology The specific epithet is dedicated to Mr. Isamu Nakajima, Mikasa City, Hokkaido, who found the specimen and gave it to us. Yezo is the feudal name for Hokkaido.

Deposition Holotype specimen (No. 890712) and micropreparations are housed in the Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University.

Terminology The terminology used to describe the vascular bundle arrangement is explained in Fig. 1.

Description It is a cylindrical petiole, 5.0×6.5 mm in diameter and 4 cm long, with 33 vascular strands arranged in an inverted omega shape in cross section (Figs. 1, 2). The epidermis consists of rectangular cells, $15–18 \times 13–17$ μm in cross section. The hypodermis is composed of 3–5-layered thick-walled cells. The cortex is double-layered. The outer cortex consists of abundant fibers and a small amount of parenchyma. The fibers are 13–27 μm in diameter with lumina 7.5–10 μm in diameter. The parenchyma cells are large, 30–49 μm in diameter, and include dispersed nests of fibers of similar size to those of the outer cortex (Figs. 3, 4). There are ca. 15 mucilage canals in the fundamental tissue except the outer cortex in cross section (Figs. 1, 2). The mucilage canals are 100–220 μm in diameter and encircled by 8–12 epithelial cells (Fig. 5). The inverted omega shape is composed of a dorsal concave crescent part (venter), high neck and long lateral collars which curves towards the ventral side (Figs. 1, 2). The vascular strand is encircled by a bundle sheath consisting of 1–2 layers of small parenchymatous cells which are rectangular with round corners, $17–30 \times 35–50$ μm in width and 50–100 μm in length (Figs. 4–8). Phloem is not well preserved. The xylem-phloem composition of each vascular bundle in cross section changes in relation to the location of the vascular bundle in the omega shape of the stele. Collateral bundles with adaxial (centripetal) xylem and abaxial (centrifugal) phloem are most common as

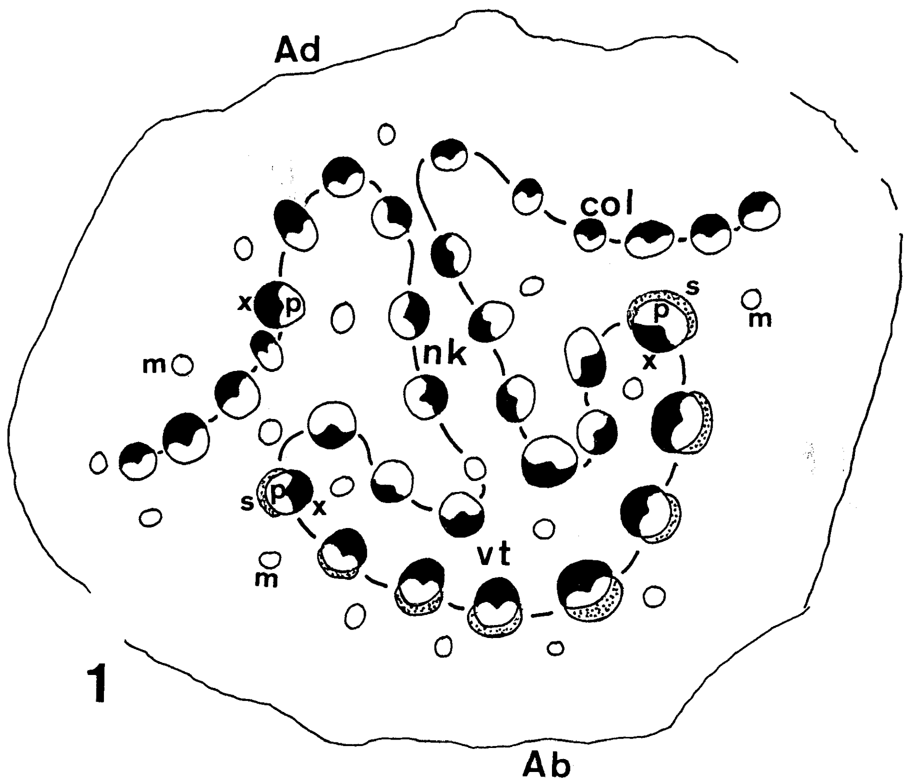
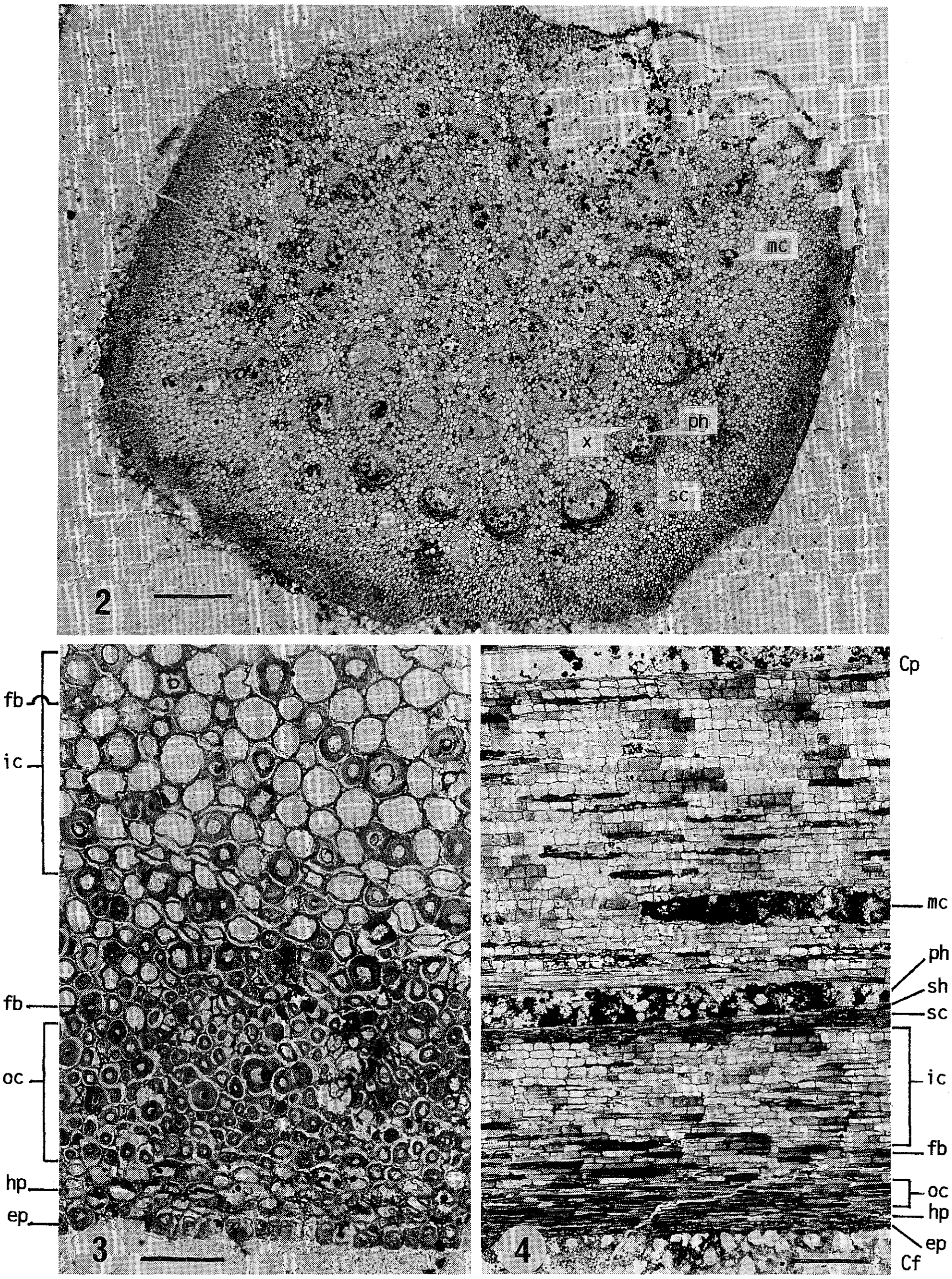


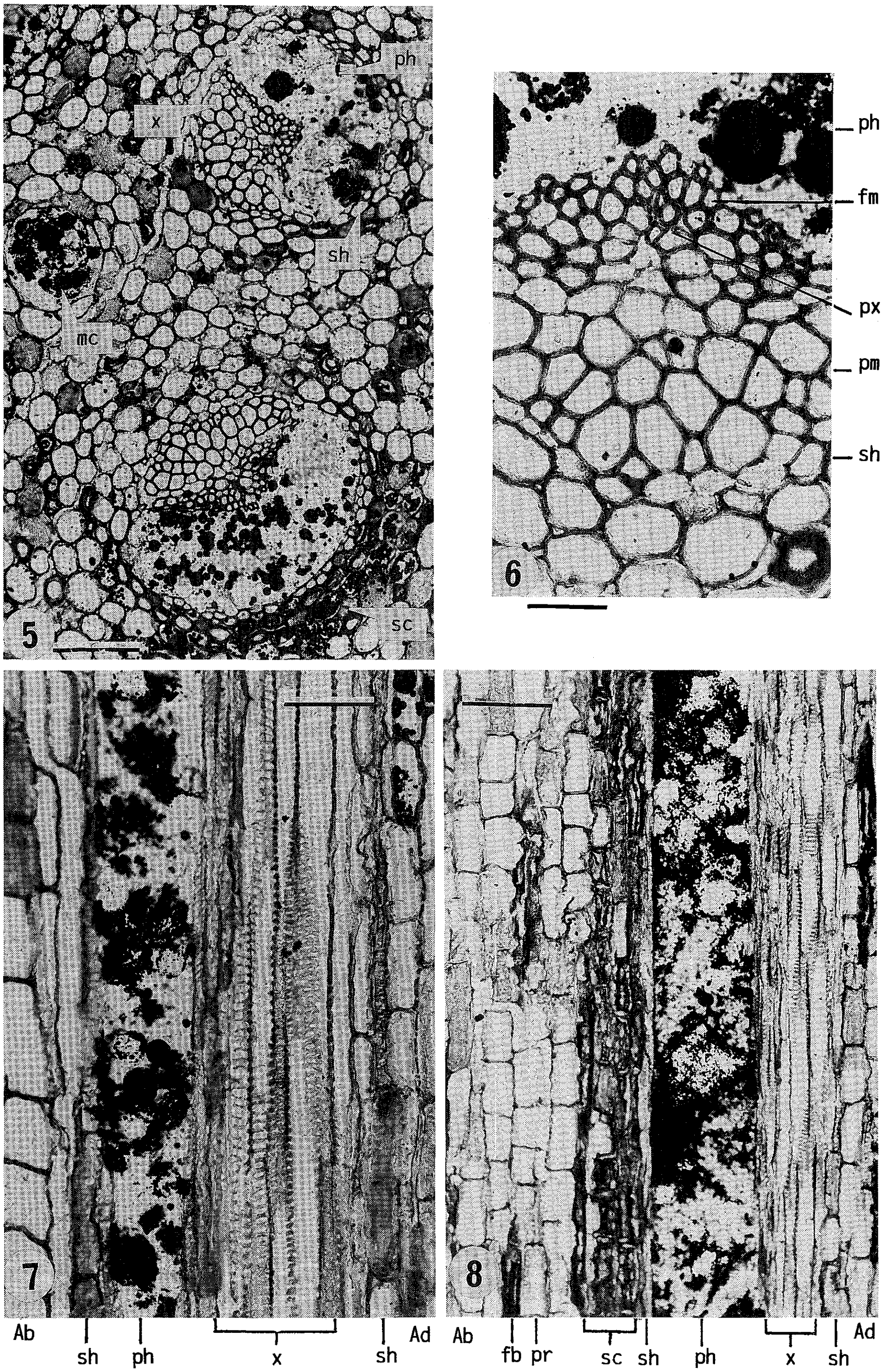
Fig. 1. Schematic figure of cross section of *Cretocycas yezonakajimae* sp. nov. showing inverted omega-shaped arrangement of vascular strands and mucilage canals, and also showing terminology of vascular arrangement. Refer to Fig. 2. Ab: abaxial side, Ad: adaxial side, col: collar, m: mucilage canal, nk: neck, p: phloem, s: sclereids, vt: venter, x: xylem. Terminology. Collar (col in Fig. 1): Group of vascular strands showing wing like arrangement at adaxial part of inverted omega-shaped arrangement of petiolar bundles. Neck (nk in Fig. 1): Longitudinally erect strands in the middle of omega-shaped arrangement. Venter (vt in Fig. 1): Group of vascular strands arranged in compressed circle or concave crescent at abaxial side of omega-shaped arrangement of petiolar bundles.

in living cycads. The xylem is centrarch, poorly developed on the phloem (centrifugal) side and well developed on the other (centripetal) side. Metaxylem tracheids are thin, 6–12 μm in diameter on the centrifugal side and are thick, 14–40 μm in diameter on the centripetal side (Figs. 5, 6). Metaxylem tracheid pitting on the radial walls is scalariform or rarely araucarian (Fig. 7). Vascular strands comprising the dorsal side of the venter of the inverted omega of the leaf trace have 2–3 layered sclereids in the outer (abaxial) side of the phloem and outside the bundle sheath, 20–30 μm thick and 100–130 μm wide (Figs. 2, 4, 5, 8). Such sclereids are lacking or only very weakly developed in other strands.

Affinity Some mesozoic cycads have been reported as petrified fossils or as impression or compression fossils. Impression or compression foliages of *Ctenis, Doratophyllum, Macrotaeniopteris, Nilssonia* and *Pseudoctenis* are identified as cycad by the stomata morphology (Florin 1933, Stewart and Rothwell 1993). *Androstrobus* from the Middle Jurassic of England (Schimper 1870, Harris 1944, 1961, 1964, Delevoryas 1962) and *Beania* from the Jurassic of England (Carruthers 1870, Harris 1941) and *Leptocycas* from the Upper Liassic of the USA (Delevoryas and Hope 1971, 1976) are compressions of male cones. *Beania*



Figs. 2–4. Fig. 2. Cross section of *Cretocycas yezonakajimae* gen. et sp. nov., showing arrangement of vascular strands. Refer to Fig. 1. Scale bar = 1 mm. Fig. 3. Magnified cross section of part of *C. yezonakajimae*, showing epidermis and cortex. Scale bar = 140 μm. Fig. 4. Radial section of part of *C. yezonakajimae*. Scale bar = 340 μm. Legend for Figs. 2–8. Ab: abaxial side, Ad: adaxial side, Cf: centrifugal side, Cp: centripetal side, ep: epidermis, fb: fibers, fm: centrifugal metaxylem, hp: hypodermis, ic: inner cortex, mc: mucilage canal, oc: outer cortex, ph: phloem, pm: centripetal metaxylem, pr: parenchyma, px: protoxylem, sc: sclereids, sh: bundle sheath, x: xylem.



Figs. 5–8. Fig. 5. Cross section of vascular strands with and without sclereids on dorsal outside of bundle sheath and mucilage canal of *Cretocycas yezonakajimae*. Scale bar = 42 μm. Fig. 6. Magnified cross section of part of vascular strand of *C. yezonakajimae*, showing less-developed centrifugal xylem and well-developed centripetal xylem. Scale bar = 21 μm. Fig. 7. Vertical section of vascular strand without outer sclereids of *C. yezonakajimae*. Scale bar = 36 μm. Fig. 8. Vertical section of vascular strand with outer sclereids of *C. yezonakajimae*. Scale bar = 72 μm.

also includes female cones (Nathorst 1909 quoted in Seward 1917, Thomas and Harris 1960, Harris 1964). *Palaeocycas* from the Upper Triassic of England is a female cone accompanied by *Bjuvia* foliage (Florin 1933). *Glandulataenia* is a fossil foliage from the Triassic of Australia (Pant 1989). To date, eight genera of petrified cycads are known. *Cycadinorachis* (Sharma 1973, Suther et al. 1986) is a petiole or rachis from the Jurassic of India. The other seven genera, *Antarcticycas* (Smoot et al. 1985), *Aricycas* (Ash 1991), *Charmorgia* (Ash 1985), *Fascisvarioxylon* (Jain 1964), *Lyssoxylon* (Gould 1971), *Michelilloa* (Archangelsky and Brett 1963) and *Sanchucycas* (Nishida et al. 1991) are all stems. The inverted omega-shaped arrangement of vascular strands, the centrarch xylem maturation, scalariform or pitted tracheids and the mucilage canals encircled by epithelial cells in the fundamental tissue are all features of Cycadales. The inverted omega-shaped arrangement of vascular bundles strengthens the cycadean affinity compared to the bennettitalean arrangement in which vascular bundles are arranged in a two-fold U-shape.

Cycadinorachis exhibits the inverted omega-shaped arrangement of vascular strands and has mucilage canals in the fundamental tissue like our fossil and most living cycads. However, the mucilage canals are smaller in *Cycadinorachis* than in our specimen or in living cycads. Moreover, *Cycadinorachis* has medullary bundles in the pith (Suther et al. 1986), which do not occur in our specimen or in most species of living cycads (Nishida and Yoshida in press). *Cycadinorachis* is also characterized by centrarch vascular bundles which are concentric and look like a protostele (Sharma 1973). *Cretocycas* also has centrarch xylem, however, the centrifugal xylem is less developed than the well-developed centripetal xylem. Living cycads, on the contrary, have mesarch bundles consisting of well-developed centripetal and poorly-developed centrifugal xylem. The centrifugal and centripetal xylem are not continuous, and are interrupted by parenchymatous cells (Nishida and Yoshida in press).

Eleven genera have been recognized in living cycads (Jones 1993). We examined their petiolar anatomy except for *Chigua* recently described by Stevenson (1990a) from The Columbian Andes. In the living genera, *Ceratozamia, Cycas, Dioon*, some species of *Encephalartos, Microcycas* and *Zamia* show inverted omega-shaped petiole bundle patterns as in *Cretocycas* (Nishida and Yoshida in press). *Macrozamia* and *Lepidozamia* principally have an inverted omega shape with modifications in the terminal parts of collars (Nishida and Yoshida in press). In *Stangeria*, the neck of the inverted omega shape consists of only one pair of strands. *Stangeria* is also characterized by crystal cells in fundamental tissue (Nishida and Yoshida in press). *Bowenia* has a rather simple arrangement of vascular strands with one medullary bundle in a vascular circle (Nishida and Yoshida in press).

Cretocycas is characterized by an outer cortex composed of abundant fibrous cells and a few parenchyma cells. Only living *Cycas* exhibits such a histology. In *Dioon* and some species of *Encephalartos*, the neck of the inverted omega shape of the petiolar traces fuses into one vertical row unlike *Cretocycas*. Therefore, *Cretocycas* closely resembles *Cycas* in the arrangement of vascular strands and in the histology of the outer cortex. *Cretocycas* is distinguished from living *Cycas* in having sclerenchymatous cells outside the bundle sheath on the phloem side, and centrarch instead of mesarch xylem. Consequently, *Cretocycas* is as a new genus of the Cycadaceae.

Discussion It should be noted that Cretaceous *Cretocycas* is histologically intermediate between Jurassic *Cycadinorachis* and living cycads. *Cycadinorachis* has a prominent centrarch vascular bundle which looks like a protostele (Sharma 1973). On the other hand, living cycads have mesarch bundles where small centrifugal xylem and large centrip-

etal xylem are separated by parenchyma (Nishida and Yoshida in press). *Cretocycas* has centrarch bundles composed of xylem which is well developed on the centripetal side, but is not interrupted by parenchyma (Figs. 5, 6). It seems to be a modification of the centrarch bundle to a mesarch bundle. The sclereids occuring outside the bundle sheath of the dorsal vascular bundles of *Cretocycas* also occur sparsely around dorsal bundles of *Macrozamia* and *Encephalartos* (Nishida and Yoshida in press).

We wish to express our thanks to Mr. Isamu Nakajima for providing the specimen. We also thank the staff of the Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University, for allowing us to use their facilities.

Endnote

1) Structure and affinities of the petrified plants from the Cretaceous of Northern Japan and Saghalien XX Contribution from the Research Institute of Evolutionary Biology, No. 111. Supported by a Grant-in-Aid for Natural History from the Fujiwara Natural History Foundation, Botany No. 29 in 1994 and 1995 to M. N.

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西田 誠, 吉田 彰, 西田治文: **北海道白亜系産ソテツ葉柄の化石による新属新種 *Cretocycas yezonakajimae***

北海道留萌郡小平町川上の小平しべ川上流から転石として採られたノジュール中より見つかった，ソテツ科の葉柄の石化化石である．独特の逆オメガ状の維管束配列をし，向軸側の翼（collar）の部分は長く，向軸側にゆるくカーブする．頸部（neck）は高く，腹部（venter: 実際には背軸側）は凹んだ半円形である（Fig. 1, 2).

現生のソテツ目植物11属中10属の葉柄と比較したが，ソテツ属に最も良く似ていた．しかし現生ソテツ目植物の葉柄維管束は中原型 mesarch であるが，本化石 *Cretocycas* は心原型 centrarch である．インドのジュラ系産の *Cycadinorachis*（Sharma 1973）によく似ているが，後者の心原型は一見原生中心柱のように後生木部が遠心方向にも求心方向にも同程度発達する．*Cretocycas* では遠心方向の後生木部は極めて小さい．*Cretocycas* の葉柄維管束はジュラ系の *Cycadinorachis* と現生のソテツ類の中間型を示すものとして注目に価する．

（[a]㈶進化生物学研究所，
[b]国際武道大学）